

Neuronal Activity Patterns in the Developing Barrel Cortex

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Abstract—The developing barrel cortex reveals a rich repertoire of neuronal activity patterns, which have been also found in other sensory neocortical areas and in other species including the somatosensory cortex of preterm human infants. The earliest stage is characterized by asynchronous, sparse single-cell firing at low frequencies. During the second stage neurons show correlated firing, which is initially mediated by electrical synapses and subsequently transforms into network bursts depending on chemical synapses. Activity patterns during this second stage are synchronous plateau assemblies, delta waves, spindle bursts and early gamma oscillations (EGOs). In newborn rodents spindle bursts and EGOs occur spontaneously or can be elicited by sensory stimulation and synchronize the activity in a barrel-related columnar network with topographic organization at the day of birth. Interfering with this early activity causes a disturbance in the development of the cortical architecture, indicating that spindle bursts and EGOs influence the formation of cortical columns. Early neuronal activity also controls the rate of programmed cell death in the developing barrel cortex, suggesting that spindle bursts and EGOs are physiological activity patterns particularly suited to suppress apoptosis. It remains to be studied in more detail how these different neocortical activity patterns control early developmental processes such as formation of synapses, microcircuits, topographic maps and large-scale networks.

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INTRODUCTION

It is well accepted that electrical activity plays a very important role in the developing brain. During so-called critical periods brain regions processing sensory information (specific brainstem and thalamic nuclei, sensory neocortical areas) undergo substantial structural and functional modifications based on the electrical activity arising from the sensory periphery (for review Erzurumlu and Gaspar, 2012; Espinosa and Stryker, 2012; Kral, 2013). These experience-dependent modifications occur at the synaptic as well as at the large-scale network level. It is often ignored that the brain reveals complex electrical activity patterns during prenatal and early postnatal development, clearly before sensory experience gained through the exploration modifies neuronal circuits during the critical periods. Although the con-

cept for the existence of a precritical period has emerged over the last decade (for review Feller and Scanziani, 2005; Khazipov and Luhmann, 2006; Blankenship and Feller, 2010), the complexity and the role of spontaneous and evoked activity patterns during earliest stages of brain development has been addressed in detail only more recently. In the spinal cord and in supraspinal circuits electrical activity is evident from the beginning of development and controls cell generation versus cell death, differentiation, axonal guidance, synapse formation, neurotransmitter specification, and the development of early circuits (for review Sanes and Lichtman, 1999; Schouenborg, 2004; Borodinsky et al., 2012; Blumberg et al., 2013; Spitzer, 2015). In the visual system, spontaneous retinal activity (“retinal waves”) triggers cortical activity and controls the formation of retinotopic maps before eye opening (Hanganu et al., 2006; Colonnese and Khazipov, 2010; Colonnese et al., 2010; Ackman et al., 2012; Xu et al., 2015). In the auditory system, spontaneous activity is present in the cochlea at early stages before hearing onset (Tritsch et al., 2007; Johnson et al., 2011; Wang et al., 2015) and controls the development of central auditory pathways. An important role of early spontaneous and evoked activity patterns has been also demonstrated in the developing somatosensory

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Abbreviations: BDNF, brain-derived neurotrophic factor; cENOs, cortical early network oscillations; CREB, cAMP response element-binding; EGOs, early gamma oscillations; FS, fast spiking; MEAs, multi-electrode arrays; SPAs, synchronous plateau assemblies; Trk, tropomyosin-related kinase; TTX, tetrodotoxin; VSD, voltage-sensitive dye.